Anatomy and Physiology of Baccharis genistelloides

By Elsie M. Kupfer

Baccharis genistelloïdes Pers. is an inhabitant of the mountains of Peru, growing in dry places at an altitude of about 1200 meters. It has several well-marked varieties which apparently spread north into Ecuador, and south and east into Brazil. The typical form is a slightly shrubby plant of extremely peculiar appearance. The leaves are atrophied, being represented by minute scales scarcely more than 2 mm. in length; and the work of photosynthesis is assumed by conspicuous wings which stand at three equal angles from each other. The scales are arranged in three orthostichies, and two wings originate from the base of each scale. One of these wings runs through only one internode and terminates at the margin of the scale below; the other, in each case, runs through two internodes until it is similarly stopped. This alternation of a long and a short wing in each orthostichy, as well as the fact that the wings (following the phyllotaxy) twist spirally, accounts for the curious appearance of the plant represented in *f. 1*.

While the shoot is almost uniformly leafless in the upper portion, usually one, two, or even several normal leaves are to be found near its base. They are of moderate size, obovate and somewhat thickened (*f. 2* and *3*). The genus *Baccharis* is a large, and as far as leaf-form is concerned, a heterogeneous one. The leaves of many species, *e. g.*, *B. floribunda* and *B. trinervis*, are large, thin and smooth; others, as those of *B. alpina* and *B. microphylla*, are minute and thickened; *B. aphylla* and *B. gracilis* have only narrow phyllodes; and, finally, *B. genistelloides* and *B. fastigiata* are devoid of foliar leaves. The leaves of several of the species, however (and it is significant that these are generally South American species), particularly *B. dioica* and *B. cassinaefolia*, closely resemble in shape, size and texture the juvenile leaves of *B. genistelloides*. There is every reason, then,

it seems to me, for considering this form as that of the ancestral type.

The seeds, unnamed, were brought from Peru by Mr. de Lautreppe in 1900 and planted

FIG. 2. Shoot from base of plant of *Baccharis genistelloides*, showing leaves.

in the New York Botanical Garden. Because of the ignorance as to their identity, little attention was given to the plants until they had attained a considerable size ; so that unfortunately none of the early stages has been ob-

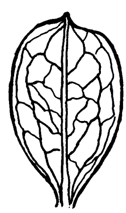

FIG. 3. Single leaf of *Baccharis genistelloides*, natural size.

served. At the present time, in the beginning of their third year, the plants are about 1 meter high. The stems near the base are secondarily thickened, and the wings there are either much thickened or have been entirely lost. Several of the plants flowered in February, 1902, and again in December, 1903 ; but although the flowers were pollinated, the seeds produced were exceedingly minute and failed to germinate.

FIG. 1. Shoot of *Baccharis genistelloides*.

Noteworthy adaptations to an environment both of strong light

and excessive dryness come to light on an examination of the anatomy and physiology of the plant.

THE EPIDERMAL SYSTEM

The protective system of the plant is very well developed. There is a considerable covering of wax over the whole plant (cf. *f. 9*). In addition, the epidermal cells are cuticularized both without and within; and particularly in the younger portions, the surface is covered with peculiar hairs, of which usually only the end-cells project above the wax. The stomata are exserted and are apparently sensitive. The *wax* is laid down in the form of irregular plates fitted together into a sort of mosaic. In the younger portions, to about 3–7 cm. back of the tip, the waxy covering is very thick, while the outer layers are shed in the form of powdery scales. Its very ready solubility in ether indicates its fatty nature. The *cutin* is present in a layer over the entire plant even up to the very tip of the growing point, though, naturally, it has less thickness here than in the older parts of the plant. The surfaces of the leaves present on the lower parts of the plant are more heavily cutinized than either the wings or the stem.

The *hairs* almost always arise in pairs from two adjacent epidermal cells. In most of the members of this family, as Vesque,* whose observations have been confirmed by more recent investigators, points out, two kinds of hairs are to be found: glandular hairs and mechanical hairs. Both kinds are present in this plant. The gland-hairs, which are composed of double series of from 3–5 cells each, differ from those mentioned by Vesque and Solereder † in that all but the end-cells contain chlorophyl. The cutin is but slightly raised by the not very abundant secretion, the nature of which has not been any more definitely determined than that it is odorless and soluble in ether (*f. 4*). That the secretion of wax is to be assigned to the epidermal cells in general, and not particularly to these hairs, seems probable from the fact that few or none of the hairs are to be found on the older portions of the plant, where, nevertheless, the wax is abundant.

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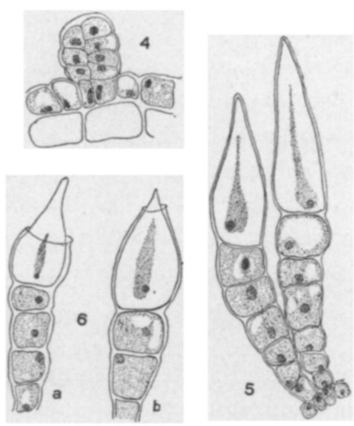
* Vesque, T. Caractères des * * * Gamopétales. Ann. Sci. Nat. Bot. VII. 1: 183. 1885.

† Solereder, H. Systematische Anatomie der Dikotyledonen. 515 ff. 1899.

The whip-hairs, too, seem to differ from the types of Vesque in that they are also, as a rule, bicollateral. They are thus apparently homologous with the gland-hairs. The early condition of the two kinds of hairs is very similar, the only difference being that the whip-hairs are from the beginning devoid of chlorophyl. In the adult condition, however, they are entirely separated from each other. The enormously enlarged end-cells have walls so highly thickened that the cell-lumen is almost obliterated (*f. 5*). The developing whip-hairs are cutinized almost from the start. When fully formed they are also uniformly covered with cutin, but there is a stage in their growth in which the base only of the end-cells is surrounded by a collar of cutin, while the thickened



Hairs of *Baccharis genistelloides*. FIG. 4. Gland-hair. FIG. 5. Two whip-hairs. FIG. 6, *a*, *b*. Developing whip-hairs.

cellulose wall of the upper part shows prominently above and through it (*f. 6 a* and *b*). Probably the cell in its period of hypertrophy breaks through its cutin covering, which is reëstablished after growth has ceased. The two whip-hairs often fail to develop simultaneously, so that a pair is frequently found, one of which is still in its prime, while the other consists of only shriveled empty cells. As far as has been determined, new hairs of either kind are not developed much below 5–6 cm. from the tip. As some also drop entirely off, the hairs on the older portions are very scattered and frequently consist of only the shriveled cells.

It is difficult to determine the function of either kind of hairs, if they have any. In the younger parts, where alone the hairs are plentiful, they are often entirely embedded in the wax. The gland-cells are usually thickly covered, while occasionally part of the end-cell of the whip-hair protrudes beyond. Of what use can a secretion be, the escape of which is entirely prevented? In the cases among the Compositae in which the whip-hairs are found, they are usually present as Vesque shows as a tomentum. Probably here, as in *Chrysoma paucifloscula* described by Professor Lloyd, they are functionless.*

The *stomata* are evidently of a motile type (*f. 7*). They are provided with distinct accessory cells, so that this plant adds another to the list of composites so provided, although Benecke † declares these cases rare. Both upper and lower walls taper into very finely pointed ridges. No trace of a hinge has been discovered by me, but the cutin seems thinner at the junction of the guard and accessory cell. The accessory cells raise the stomata somewhat above the level of the epidermis. They are more exserted on the stem than on the wing.

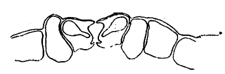


FIG. 7. Stoma from stem of *Baccharis genistelloides*.

THE STEM

In the plants examined, the stem varies in thickness from 1 to 4 mm. In the younger portions, to about 12 cm. from the tip, the supporting tissue consists largely of sclerenchyma, the wood proper being confined to a very narrow ring about 25 μ in diameter. The masses of bast-fibers are found at intervals around the stem, but the six largest masses are opposite the three wings and half way between them respectively (*f. 8*). These bast-fibers are strongly lignified, so that they give a much more pronounced reaction with phloroglucin than the young wood-ring itself. The lignification of the bast-fibers begins very near the growing tip; signs of it can be found at the distance of 1.5 cm. therefrom. This early acquisition of lignin would seem to indicate a very slow rate of growth — a point which will be recurred to presently.

* Lloyd, F. E. Anatomy of *Chrysoma paucifloscula*. Bull. Torrey Club, **28**: 445. Au 1901.

† Bot. Zeit. **50**: 570. 1892.

The bast-bundles lie so close to the circle of wood — a feature according to Solereder characteristic of the Compositae — that no cambium was distinguishable as such in any portion of the stem of the growing plants. There are a number of thin-walled irregular cells between wood and bast, most of which are sieve-tubes; but some must be of a meristematic nature, because the wood-cylinder gradually increases in diameter so as to be about 60 mm. at a

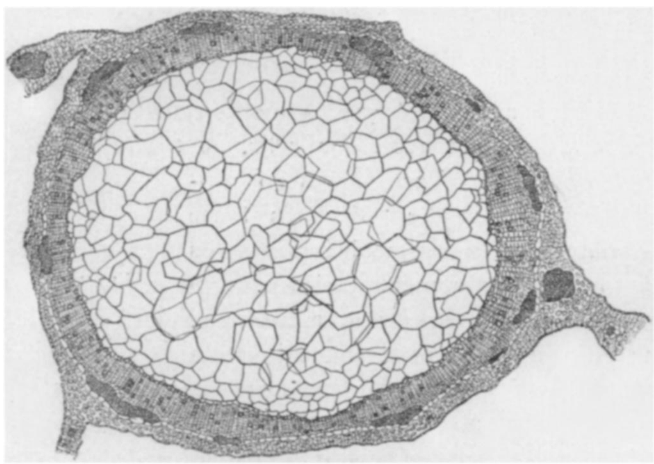


FIG. 8. Cross-section of stem of *Baccharis genistelloides*.

distance of 15 cm. from the tip, 125 mm. at 19 cm., and 166 mm. at the base of the plant examined.

In an older stem taken from a herbarium specimen there were present three definite wood-rings and a very clearly established cambium layer. The wood on maceration was found to contain spiral, pitted and annular vessels. Wood parenchyma is abundant, but the medullary rays are obliterated. Around the primary bast-masses when they occur, otherwise external to the sieve tissue, an endoderm of one layer of rather large clear cells extends. Outside of this lies the cortex, of three or more rows of chlorophyl-bearing cells. Outside of the bast-bundles, however, these cells lose their chlorophyl and become collenchymatic. The angles of the older stems from which the wings have been lost become heavily suberized.

APOGEOTROPISM

The stems of *Baccharis genistelloides* are markedly apogeotropic. A number of the branches of plants which have been grown in a moist greenhouse have fallen down from their own weight. In all cases, however, the tips have turned perpendicularly upwards, and the plants present a very striking appearance in consequence. They are markedly different from the diageotropic shoots of *B. halimifolia*, which is growing in the same place. That this falling down of the branch is also characteristic of the plant in its natural environment is seen from herbarium specimens. There are often as many as six upright branches from one prostrate one.

THE WING

The wings are the conspicuous portion of the plant; they vary in width from a few millimeters at the youngest portions to 2 cm. at the older. The length depends upon their relation to the internodes. As shown above (*f. 1*) some wings go through only one, others through two internodes, the longer ones being from 10–18 cm., the shorter from 3–8 cm. A transverse section (*f. 9*) shows a very compact structure. There is no definite palisade or spongy tissue. Several rows of chlorophyl-bearing cells packed more or less closely extend inward from both surfaces. The air spaces, which are comparatively few, are chiefly situated in the middle of the wing. The stomata are approximately equal in number on both sides of the wing, averaging 70–80 to the square millimeter.

The wings are notably rigid; this is due to the occurrence of strands of mechanical tissue which are developed in connection with the vascular bundles. The conducting tissue plays but an unimportant rôle in the support of the wing. There is a particularly large stereome mass on the extreme edge, which is readily removable as a thick thread.

In order to determine the morphology of the wing, serial sections of the growing point were prepared. From these it appeared that the wings are directly continuous with the margins of the scales. On comparison with shoots bearing true leaves this view was substantiated. In the terms of many of the text-books, then, these wings would stand as "decurrent leaves" — as elaborations

of the leaf-base, named by Vines the "hypopodium." Their peculiar phyllotactic arrangement would thus obviously be explained. The question was raised however as to whether these facts alone, *i. e.*, the connection with the leaf-base and their phyllotactic relation, would be sufficient to establish the homology with leaf-structures. The point was decided in the negative for the following reasons:

1. Their main axes, even at the growing point, are parallel to the stem, instead of at a greater or less angle as in other developed leaf-bases, *i. e.*, stipules.

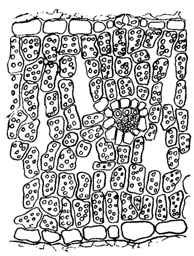


FIG. 9. Cross-section of wing of *Baccharis genistelloides.*

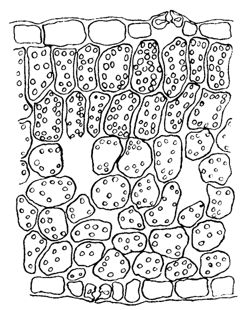


FIG. 10. Cross-section of leaf of *Baccharis genistelloides.*

2. In many plants, *Lathyrus latifolia*, *L. sylvestris* and *L. grandiflorus* among others, both stipules and wings occur. In such cases the wings, although just as obviously continuous with the wings of the petiole, evidently could not be hypopodia.

3. Other organs have been found that follow the leaf arrangement, but may not therefore be supposed to be leaf-structures — for example the thorns in some species of *Rubus* and *Smilax*, the ridges in the stems of *Urtica gracilis*, *Mentha crispa* and *Leptandra Virginica.*

For these reasons the wings are, it seems to me, rather to be regarded as lateral-vertical expansions of the stem than as "decurrent leaf-margins."

PHOTOTROPISM

To determine the action of the plant towards light a growing shoot was fastened in a dark chamber illuminated from one side only. After fourteen days there was found to be a decided photo-

tropic reaction. The stem had turned towards the light, the bending region extending to about 3 cm. from the tip. The two wings nearest the aperture had turned at right angles to each other and in the direction of the rays, the third wing had moved to a position just behind and parallel to one of the others. In this way only its very edge was illuminated. Although at first it seemed as if the wings must have played a positive part in the movement towards the light, probably a purely mechanical explanation is to be assigned for their position. By experiment it was found that these would be the positions assumed by any rigid objects — such as strips of cardboard — fastened to a bending axis, so that probably only the stem was directly concerned in the reaction.

THE LEAF

The leaves themselves vary in size. The largest found measured 2.2×1.3 cm., the smallest 5×3 mm. (*f. 3*). They appear, as above pointed out, at the basal portion, but also occasionally on new shoots, developing from buds on these regions. A transverse section of the leaf (*f. 10*) shows that here also we have a fairly compact mesophyl structure. The intercellular spaces are, as in the wings, comparatively small. In the leaf, however, sharply distinguishing it from the wings in structure, we find a noticeable dorsi-ventral differentiation; for not only has the leaf a definite palisade parenchyma of two layers of cells, but a difference is also to be observed in the number of stomata present on the two surfaces. There are 106 stomata to the square millimeter on the lower surface to 50 on the upper. It is to be noted as significant that the whole number of stomata per square millimeter would average almost exactly the same in the case of the wing and the leaf.

REVERSION TO THE JUVENILE LEAF-FORM

Several experiments were started with a view to inducing the re-formation on adult shoots of the juvenile leaf-form. Some of the growing shoots were kept in a moist chamber, others in a dry and still others in a dark chamber for several weeks, but no results were obtained. This may have been due to one or more of several causes. First, of course, these particular agents may not induce leaf-formation in this plant; or again the failure may have been

due to the fact that growing shoots (and therefore shoots very far from the usual basal region of leaf-production) were used; or finally, it may have been due to the fact that all the shoots which were experimented with formed flower-buds on being released, as it is believed that when a shoot has once laid down the primordium of a flower it is thereafter unchangeable.

To avoid the repetition of these conditions it was determined to defer the experiments until such a time as separate plants would be available for the different experiments. For this purpose, but also more particularly to determine the effect upon the leaf-reversion, a large number of cuttings were made, consisting, of course, of the youngest shoots, *i. e.*, those farthest from the juvenile character. The cuttings were difficult to root; less than half of those planted at three different times succeeded. At present, however, there are about 15 more or less healthy young plants.

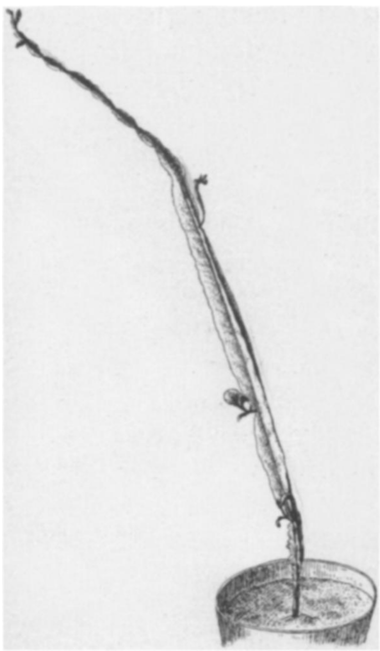


FIG. 11. Cutting of *Baccharis genistelloides*, showing production of juvenile leaves.

On three of the cuttings which were planted earliest, reversion shoots of a remarkable character developed. The first one to be affected produced from buds two branches, on each of which appeared three reversion leaves, and on which the wings were reduced almost to a minimum. Also (and this seems extraordinary) the main shoot produced near its apex several smaller leaves. This is the plant represented in *f. 11*.

On the second plant a similar set of phenomena was observable. Three shoots bearing some of the largest leaves that have been found and the greatly reduced wings appeared, and at the same time the tip of the shoot continued to produce leaves as it grew.

On the third the main shoot withered; and one of the buds produced a branch on which the wings are apparently normal, but on which three small leaves have been found. Four other plants produced leaves on branches that retained their wings.

The apogeotropic habit of the secondary branches made another experiment possible. A plant on which the main branch had fallen from its own weight and on which there were a number of such upright shoots was layered — that is, had its main stem covered with earth. After allowing the branches to rest in this condition for some time, the connection of the vertical shoots with one another and with the main stem was severed. However, although all the shoots flourished and grew into separate plants, none produced the leaves.

To sum up briefly the most important points brought out in this investigation:

1. *Baccharis genistelloides* is a plant remarkably well adapted by the loss of leaves, by the position of the wings, and by the coverings of the cutin, wax and hairs, to withstand a high degree of both dryness and insolation.

2. The glandular hairs differ from the hairs previously described in the Compositae in the possession of chlorophyl, and the whip-hairs in being biserial.

3. The early acquisition of lignin in the bast of the stem, and of mechanical tissue in the wings, gives to the plant its characteristic rigidity, and at the same time necessitates a short period of elongation.

4. The leaves found in any given portion of the stem on the older parts of the plant resemble closely the leaves of other species of *Baccharis*.

5. The leaf differs from the wing in structure in showing marked dorsiventrality, which is absent in the latter.

6. While the wings are directly continuous with the margins of the scales and of the leaves when present, and while they follow the phyllotaxy, they are to be considered morphologically as lateral-vertical expansions of the stem and not as "decurrent leaves."

7. The shoots have been shown to be markedly apogeotropic and positively phototropic.

8. Cuttings of growing shoots were made, a number of which after rooting produced branches which bore reversionary leaves and greatly reduced wings ; the apices of the old shoots also produced the leaves in two cases.

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